

Anoplophora glabripennis (Coleoptera: Cerambycidae) Fecundity and Longevity Under Laboratory Conditions: Comparison of Populations from New York and Illinois on *Acer saccharum*

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ABSTRACT Reproductive traits and longevity of *Anoplophora glabripennis* (Motschulsky) from the Ravenswood, Chicago, IL, and Bayside, Queens, NY, populations were compared for first-generation adults that emerged from cut infested wood and for second-generation adults that were reared on artificial diet. Illinois females were significantly more fecund than those from New York when they emerged from infested wood and tended to be more fecund when reared on artificial diet. Weights of adult females that emerged from infested wood varied with the hosts they emerged from; but when reared on artificial diet, Illinois females were significantly heavier than New York females. There were no significant differences between the two populations in egg viability or adult longevity. In general, females laid more eggs and survived longer in the laboratory on sugar maple, *Acer saccharum* Marshall, than has generally been reported for this tree species. Larval food source and quality had significant effects on female fecundity and longevity. The above differences between the two populations and the effects of host quality and host species should be taken into account when management decisions are made in the current eradication program for *A. glabripennis* in the United States.

KEY WORDS *Anoplophora glabripennis*, fecundity, longevity, host effects

Anoplophora glabripennis (Motschulsky), referred to as Asian longhorned beetle in the United States, is one of the more recently introduced non-native invasive species to become a major pest in the United States. It was first discovered in Amityville and Brooklyn, NY, in 1996 (Haack et al. 1997). In 1998, it was found in three separate locations in the Chicago, IL, metropolitan area (Poland et al. 1998). It has since been found in Queens, Flushing, and Manhattan in the New York City metropolitan area, Islip on Long Island, and Park Ridge, O'Hare Airport, and the Kilbourn Park area in Chicago (Poland et al. 2001).

In the United States, the USDA Animal and Plant Health Inspection Service (APHIS) has implemented an eradication program whereby all trees with signs of beetle infestation (oviposition pits or exit holes) are removed and destroyed. The eradication program for *A. glabripennis* has greatly impacted the environment in the cities where it has been found (thousands of trees removed), and the eradication program has cost millions of dollars (Nowak et al. 2001). The United States has placed restrictions on trade to prevent further introductions (USDA-APHIS 1998). If the populations of *A. glabripennis* are not eradicated in the United States, the beetle could threaten the maple sugar industry, fall-foliage tourism, and many beloved

backyard and street trees (USDA 1999, Nowak et al. 2001).

Anoplophora glabripennis is widely distributed in China, and is present in Korea. In China, it is considered a major pest of several deciduous broadleaf tree species (Xiao 1992). It causes severe damage from 21 to 43° N latitude and 100 to 127° E longitude (Yan 1985). Its primary host trees in China include species of *Acer* (maple), *Populus* (poplar), *Salix* (willow), and *Ulmus* (elm), and is reported to feed on >24 species of hardwood trees (Yang et al. 1995). In parts of China, *Acer negundo* L. (boxelder) and *Acer saccharum* Marshall (sugar maple), two North American maple species, are used as trap trees to protect more valuable hardwood trees from attack (Sun et al. 1990). In China, *A. glabripennis* takes 1 or 2 yr to complete development depending on the timing of adult emergence; later emerging adults lay eggs that may not hatch until the next spring (Fan et al. 1997). Field-collected females live an average of 46 d on *Acer negundo* L., and 9 d on I-69 *Populus* in the laboratory, whereas males live an average of 13 and 8 d on *A. negundo* and I-69 *Populus*, respectively (Gao and Zheng 1998). In the laboratory, females laid an average of 32, 20, 24, and 23 eggs over their lifetime on *A. negundo*, *Populus canadensis* Moench, *Salix matsudana* Koldz, and *Acer truncatum* Bunge, respectively (He and Huang 1993).

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Although the general life history of *A. glabripennis* has been documented in China, there is a critical need for more detailed information on the basic biology of *A. glabripennis*, specifically in North America and on North American hosts. This information is needed to predict the timing of biological events fundamental to the development and improvement of exclusion and eradication methodologies. Knowledge about the beetle's fecundity is important to understanding its population dynamics and predicting population growth. The tree species on which the adult beetles feed also has been shown to affect fecundity (He and Huang 1993; Smith et al. 2001).

Here the fecundity, egg viability, and longevity of *A. glabripennis* adults from the two populations in the United States are compared on *A. saccharum*, both for beetles from infested wood and for their progeny reared on artificial diet. Daily, weekly, and lifetime oviposition of the females from each population are compared.

Materials and Methods

Populations. The majority of the first-generation adults used in these studies emerged directly from infested branch sections; however, a few were reared to adulthood on artificial diet after being removed as large larvae from the infested logs. The infested branch sections were obtained in February 1999 from the Ravenswood, Chicago, IL, and April 1999 from the Bayside, Queens, NY. Branch sections were transported under permit to the USDA-Forest Service quarantine facility in Ansonia, CT, where all the research was conducted. The branch sections were measured then held at $20 \pm 5^\circ\text{C}$ and $50 \pm 10\%$ RH in heavy trash barrels with screened holes in the lids for ventilation. Newly emerged beetles were removed from the barrels twice daily. The beetles were weighed and sexed before they were presented with twigs to feed on and were allowed to mate. The progeny of these matings were reared on artificial diet to produce the second-generation adults.

The number of mating pairs from each generation and population varied among studies. Sixty, first-generation and 29 second-generation mating pairs from Illinois and 39 first-generation and 24-second generation pairs from New York were used to assess weekly oviposition, egg viability, fecundity, and female longevity. Twenty additional first-generation mating pairs from both populations were used to assess daily oviposition over the first 5 wk on bolts that were changed weekly. Finally, 20 additional second-generation pairs from the Illinois population were used to compare daily oviposition rates between bolts changed weekly (eight pairs) and daily (12 pairs).

Voucher specimens of the two *A. glabripennis* populations were deposited at the Entomology Division, Yale Peabody Museum of Natural History, New Haven, CT.

Rearing Methods. Larvae removed from infested bolts and the progeny of the first generation were reared on an artificial diet developed for *Enaphalodes*

rufulus (Haldeman) (Galford 1985). Larvae were held individually at $25 \pm 2^\circ\text{C}$ and $60 \pm 5\%$ RH in the dark in clear plastic jars (59, 118, or 237 ml, depending on the larva's size) and the diet was changed every other week. Pupae were held in 50-ml containers in a water box (50 by 40 by 25-cm opaque plastic boxes with grating in the bottom to support containers above the water) until adult emergence.

Virgin adults were held individually in 950-ml glass jars with *A. saccharum* twigs until mated. Adults used in the daily fecundity studies were fed for an average of 7 d before mating to ensure prompt egg laying once mated (adults typically do not begin to oviposit until the second week of feeding). First-generation adults used in the weekly fecundity study were mated within 24 h of emergence, and the second-generation adults were fed an average of 8 d before they were mated. The time before mating was variable because adults emerged over a long period of time and a mate was not always available immediately.

Each pair of adults was individually mated in a 3.8-liter glass jar. *Acer saccharum* twigs were added twice a week as a food source; twigs were cut fresh weekly. Freshly cut *A. saccharum* bolts (3–7 cm diameter and 20 cm long) with both ends waxed were provided to the mating pairs for oviposition.

The oviposition bolts were replaced weekly until all the females died (3–15 wk) except in the daily oviposition study where they were changed daily for a period of 2 wk (weeks 2–3 after mating). To determine daily oviposition for the set of pairs where the bolts were changed weekly, the logs were checked daily and each new oviposition pit chewed in the bark was labeled with a mark specific for the day of the week. All pits chewed in the bark (both pits that obviously contained eggs and those that did not) were counted and the bolt diameter was measured when the oviposition bolts were removed. Adult mortality was checked twice a week for pairs that were not part of the daily oviposition study.

Oviposition and Egg Variability. After removal from mating jars, the bolts were held at $25 \pm 2^\circ\text{C}$ and $60 \pm 5\%$ RH until the bark was stripped and all eggs and larvae were counted. Eggs are laid beneath the bark and early larval instars feed under the bark, whereas later instars enter the wood. All bolts used to determine daily oviposition were stripped 6 d after being removed from the adults to obtain eggs of known age for other studies. Eggs removed from under the bark were placed in vented 15 by 60-mm petri dishes that were held in water boxes at $25 \pm 2^\circ\text{C}$ for 3 wk and checked daily for hatch. All bolts used to determine weekly oviposition were held a minimum of 3 wk after removal from the mating pairs of beetles before stripping the bark to allow viable eggs to hatch. Eggs that hatched, either before or after being removed from under the bark, were considered to be viable.

Statistical Analyses. Analysis of variance (ANOVA) (PROC GLM, SAS Institute 1990 or one-way ANOVA, Statistix 1998) was used to determine if significant effects existed. The least significant difference (LSD) mean separation test with $\alpha = 0.05$ was used to com-

Table 1. Comparison of fecundity, egg viability, and longevity of *Anoplophora glabripennis* females from the Bayside, NY, and Ravenswood, IL, infestations using *Acer saccharum* twigs for food and bolts for oviposition

Character (mean \pm SE)	Bayside, Queens, NY		Ravenswood, Chicago, IL	
	1st generation	2nd generation	1st generation	2nd generation
Lifetime fecundity	51.0 \pm 4.3 b	72.7 \pm 7.4 a	68.1 \pm 4.0 a	74.8 \pm 8.0 a
Eggs/d	0.63 \pm 0.05 b	0.82 \pm 0.07 a	0.93 \pm 0.04 a	0.92 \pm 0.09 a
Lifetime viable eggs	45.1 \pm 4.2 b	56.9 \pm 5.7 ab	61.7 \pm 4.0 a	57.3 \pm 6.9 ab
Lifetime % viable eggs	88.8 \pm 2.5% a	80.0 \pm 2.5% b	88.6 \pm 1.4% a	73.8 \pm 2.7% b
Lifetime pits chewed	304.2 \pm 18.9 a	218.0 \pm 20.9 b	270.2 \pm 13.6 ab	293.9 \pm 29.4 a
Lifetime % pits with eggs	16.9 \pm 1.3% c	35.3 \pm 2.3% a	25.7 \pm 1.1% b	25.6 \pm 1.7% b
Female longevity (d)	79.3 \pm 2.3 ab	88.0 \pm 3.3 a	72.6 \pm 2.3 b	81.0 \pm 4.0 a
Male longevity (d)	—	106.2 \pm 4.4 a	—	99.3 \pm 7.3 a
Emergence weight (g)	1.04 \pm 0.05 c	1.40 \pm 0.09 b	0.85 \pm 0.03 d	1.64 \pm 0.08 a
n	39	24	60	29

An egg was considered to be viable if it was able to hatch. Means within each row followed by the same letter are not significantly different based on an LSD mean separation test with $\alpha = 0.05$ (Statistix 1998). —, Data not available for first generation.

pare means within each significant factor in the ANOVA (Statistix 1998). A repeated measures ANOVA (PROC GLM, SAS Institute 1990) was used to compare weekly and daily means between *A. glabripennis* populations within each generation for oviposition and number of pits chewed in the bark. Linear regression (forced through the origin) was used to look for significant relationships between longevity and fecundity, female emergence weight and fecundity, and longevity and female emergence weights.

Results

Oviposition. First-generation Illinois adult females that emerged from infested wood laid significantly more eggs over their lifetime, both in total number and on average per day, than New York females. There were no differences in the number of eggs laid between the two populations in the second generation reared on artificial diet (Table 1). In the first generation, Illinois females laid significantly more eggs per week on average than the New York females during the first through fourth weeks (week 1, $F = 5.92$; $df = 1, 96$; $P = 0.0168$; week 2, $F = 21.87$; $df = 1, 96$; $P = 0.0001$; week 3, $F = 13.40$; $df = 1, 96$; $P = 0.0004$; week 4, $F = 6.08$; $df = 1, 96$; $P = 0.0155$; GLM repeated measures SAS Institute 1990; Fig. 1). There were no significant differences between populations in the mean eggs laid per week during the second generation but the Illinois population tended to lay more eggs per week during the third through seventh weeks (Fig. 1). Although no statistical comparison could be made for mean weekly oviposition between the two generations because of differences in the premating feeding times, there were two apparent effects of the longer premating feeding period in the second generation—more eggs were laid in the first week after mating, and the peak of the egg laying during week 3 was higher than in the first generation (Fig. 1). The peak egg-laying period occurred during the third week after the female emerged and began feeding in both generations for the Illinois population and in the first generation for the New York population (Fig. 1). The peak egg-laying period for the second generation of

the New York population occurred during the second week.

Days to first oviposition in the first generation were similar for both populations, 9.1 ± 1.0 d for New York females and 9.9 ± 0.8 d for Illinois females. Time to first oviposition was not affected by the mating time within the first 9 d. Several females that had a week or more of feeding time before they were mated laid their first egg within 24 h of mating and these eggs were viable. The highest number of eggs laid in a single day was 11 for Illinois females and 10 for New York females. A second-generation Illinois female had the highest fecundity with 170 eggs, of which 157 were viable. As for weekly oviposition rate, peak daily oviposition oc-

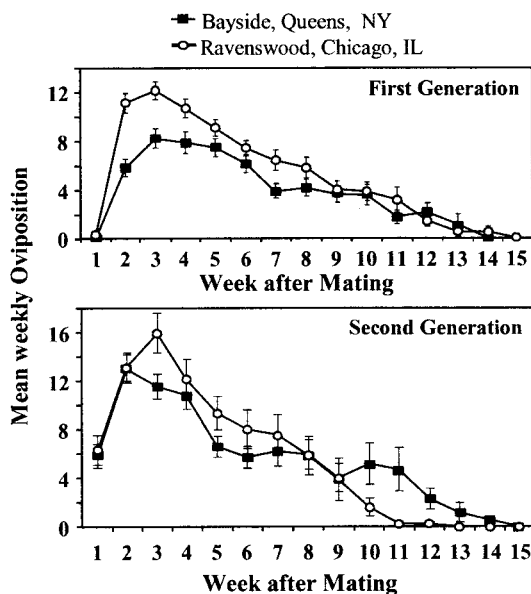


Fig. 1. Mean \pm SE weekly oviposition after mating of females from Ravenswood, Chicago, IL, and Bayside, Queens, NY, for two generations held at $25 \pm 2^\circ\text{C}$ and $60 \pm 5\%$ RH. First-generation individuals emerged from infested cut wood from each site and second-generation individuals were reared on artificial diet.

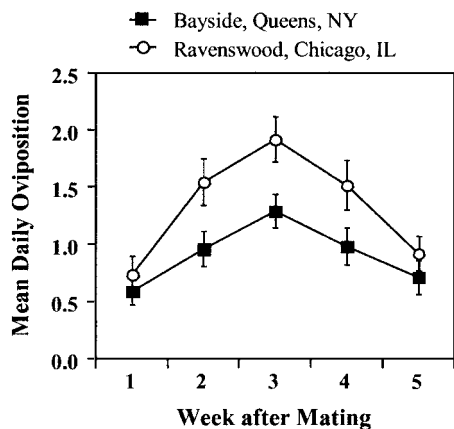


Fig. 2. Mean \pm SE daily oviposition by week after mating of females from Ravenswood, Chicago, IL, and Bayside, Queens, NY, that emerged from infested cut wood and were held at $25 \pm 2^\circ\text{C}$ and $60 \pm 5\%$ RH.

curring during the third week for both populations and generations (Fig. 2). A second-generation Illinois female, whose logs were changed daily, had the highest third week average with 5.3 eggs per day. The diameter of the oviposition bolt used (3–7 cm) did not have a significant effect on the number of eggs a female would lay on the bolt, but the trend was that more eggs were laid on larger bolts.

Over the first 5 wk during the first generation, the average daily oviposition of Illinois females was greater than that of New York females (Fig. 3). During each of the 5 wk that daily oviposition was followed for both populations, peak daily oviposition occurred on the first day the new bolt was put in the mating jar (Fig. 3). Average daily oviposition of the Illinois females was significantly higher than that of the New York females during the second ($F = 5.34$; $df = 1, 38$;

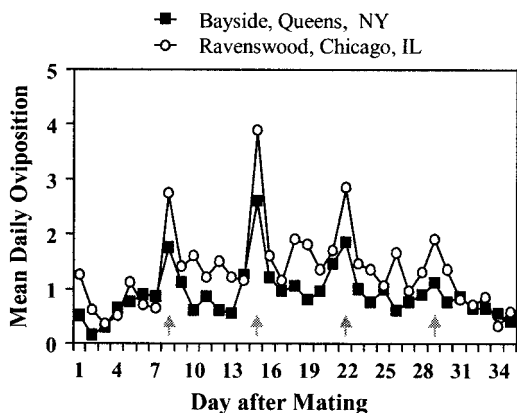


Fig. 3. Mean \pm SE daily oviposition after mating of first-generation females from Ravenswood, Chicago, IL, and Bayside, Queens, NY, that emerged from infested cut wood and were held at $25 \pm 2^\circ\text{C}$ and $60 \pm 5\%$ RH. Oviposition logs were replaced weekly. Arrows indicate days immediately following oviposition log replacement.

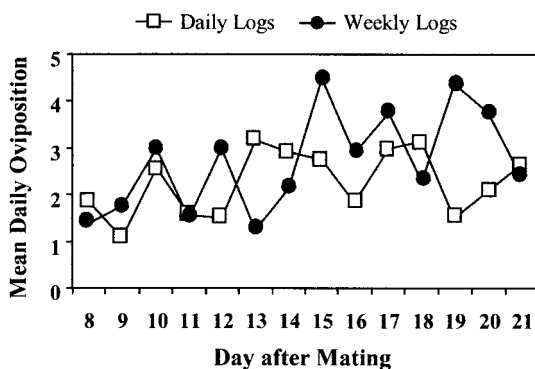


Fig. 4. Mean \pm SE daily oviposition 8–21 d after mating of second-generation females from Ravenswood, Chicago, IL, that were reared on artificial diet and were held at $25 \pm 2^\circ\text{C}$ and $60 \pm 5\%$ RH. Oviposition logs were either changed daily or weekly (days 7, 14, 21).

$P = 0.0263$; GLM repeated measures SAS) and third weeks ($F = 6.48$; $df = 1, 38$; $P = 0.0151$; GLM repeated measures SAS Institute 1990) (Fig. 2).

The average second-generation daily oviposition of Illinois females for weeks 2 and 3 was significantly higher ($\alpha = 0.05$, critical t value 1.969, LSD Statistix 1998) when the oviposition bolt was changed weekly (2.7 eggs/d) rather than daily (2.2 eggs/d, Fig. 4). Daily oviposition rates fluctuated randomly throughout the 2 wk, with no pronounced peak on the days when the weekly bolts were changed (Fig. 4).

A significantly higher percentage of eggs laid by both populations were viable in the first generation than in the second generation (Table 1; Fig. 5). Mean percentage viability by the week the egg was laid was constant over most of the female's lifetime but tended to drop slightly toward the end (Fig. 5). Most females did not lay any eggs during the last week of their life. Females lived an average of 10–13 wk.

Females from both populations during both generations chewed many oviposition pits in the bark in which no egg was laid. The percentage of pits in the bark containing eggs did not differ by generation for the Illinois population but was higher for the second than the first generation for the New York population (Table 1). The mean number of pits chewed weekly for both populations during the first generation mirrored the pattern for the mean weekly oviposition (Figs. 1 and 6). There were no significant differences in the mean number of pits chewed weekly by the two populations but the New York population females did have a higher peak number of pits chewed (Fig. 6). Females from both populations chewed an average of 10–20 pits in the bark during the first week after mating when few if any eggs were laid.

Longevity. Second-generation females from both populations lived longer than those in the first generation, but the difference was only significant for the Illinois population (Table 1). There were no significant differences in male longevity between the populations in the second generation and data for the first

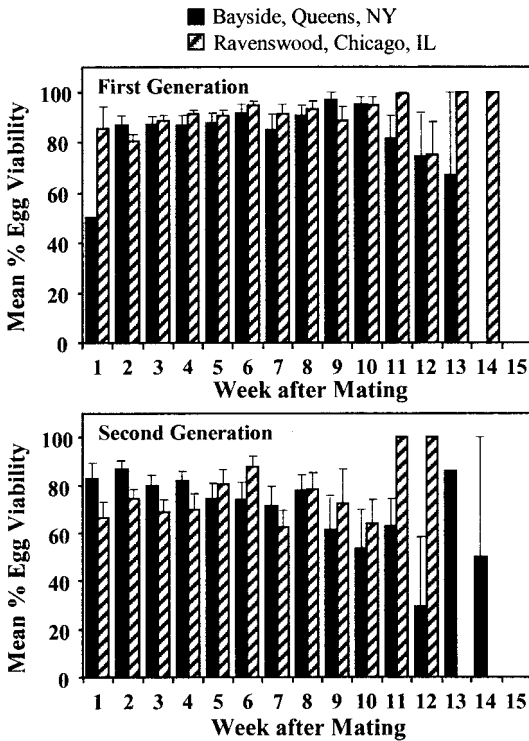


Fig. 5. Mean \pm SE percentage egg viability by week after mating for two generations of females from Ravenswood, Chicago, IL, and Bayside, Queens, NY, that were held at $25 \pm 2^\circ\text{C}$ and $60 \pm 5\%$ RH. First-generation individuals emerged from infested cut wood from each site and second-generation individuals were reared on artificial diet.

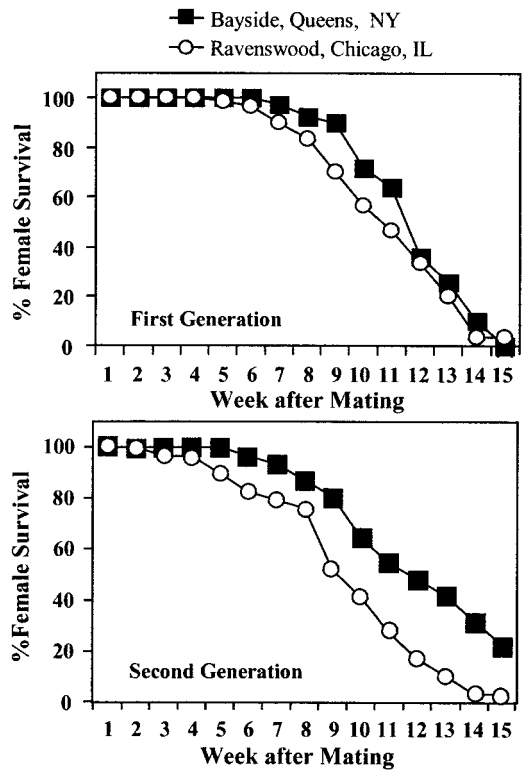


Fig. 7. Weekly percentage survival after mating for two generations of females from Ravenswood, Chicago, IL, and Bayside, Queens, NY, that were held at $25 \pm 2^\circ\text{C}$ and $60 \pm 5\%$ RH. First-generation individuals emerged from infested cut wood from each site and second-generation individuals were reared on artificial diet.

generation were not available for males. Illinois female survival dropped to 50% in the first generation at 10 wk and in the second generation at 9 wk (Fig. 7). Survival of New York females dropped to 50% at week 11 in both generations but more second-generation females were still alive after 13 or more weeks than in the first generation (Fig. 7).

Fecundity. Longevity had a strong positive correlation with female fecundity. Longer-lived females

were able to mature and lay more eggs. Linear regressions of the influence of fecundity on longevity through the origin (Statistix 1998) showed that egg per day rates were equivalent to the actual measured rates for both generations (Table 1; New York first generation $y = 0.65x$ (y = fecundity, x = longevity in days, and $r^2 = 0.83$), New York second generation $y = 0.84x$ ($r^2 = 0.86$), Illinois first generation $y = 0.95x$ ($r^2 = 0.90$), and Illinois second generation $y = 0.93x$ ($r^2 = 0.82$)).

Body Size. New York females were significantly heavier than those from the Illinois population when they emerged from wood (first generation) but the reverse was true when the females were reared on artificial diet (second generation) (Table 1). Female weight did not have a significant effect on longevity. However, female weight was positively correlated with female fecundity. When data for the two generations of each population were combined and analyzed by linear regression through the origin, the Illinois population had a per gram fecundity rate of 63 ± 4 eggs/g adult female weight ($r^2 = 0.82$), whereas the New York population had a rate of 47 ± 3 eggs/g adult female weight ($r^2 = 0.77$).

Effect of Host Species and Branch Size. The tree species from which the first-generation adult females

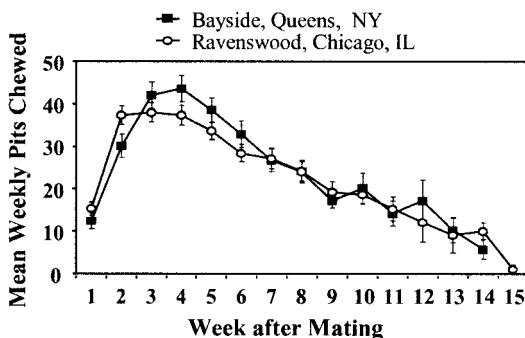


Fig. 6. Mean \pm SE weekly oviposition pits chewed in the bark after mating for females that emerged from infested cut wood and were held at $25 \pm 2^\circ\text{C}$ and $60 \pm 5\%$ RH.

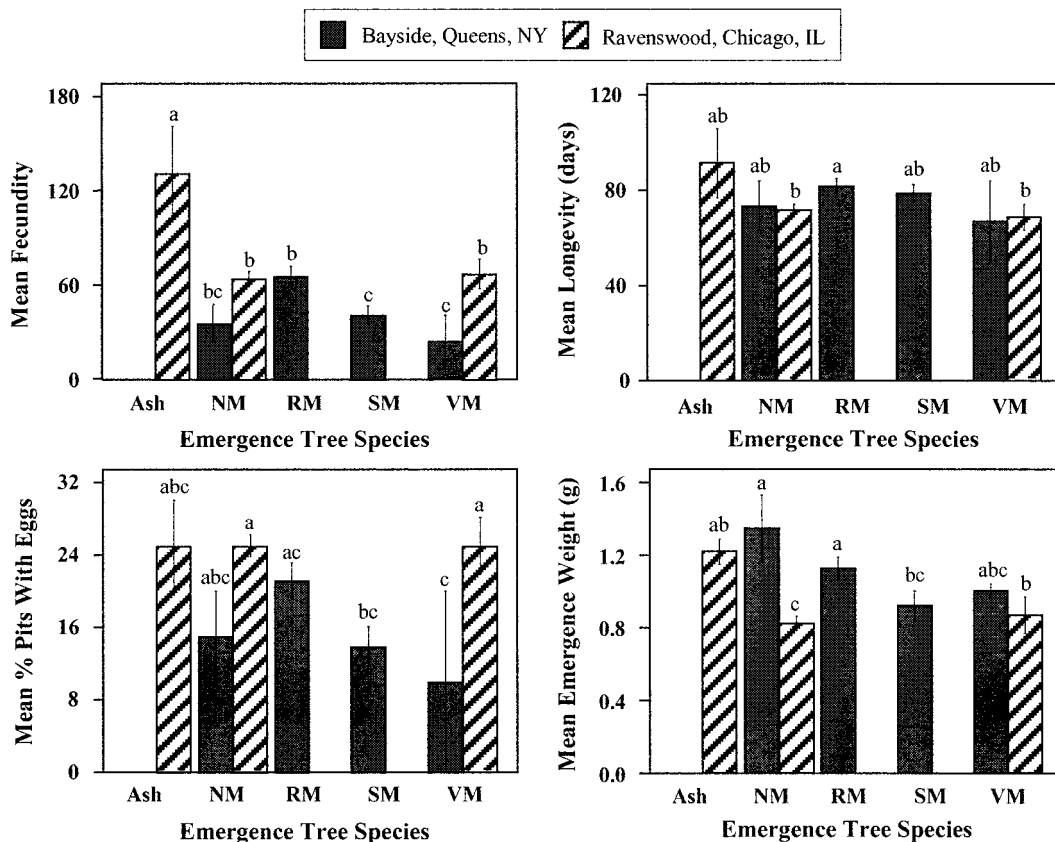


Fig. 8. Effects of tree species from which females emerged on mean \pm SE female fecundity, longevity, and emergence weight, and percentage of pits females chewed in the bark that had eggs laid in them. Females emerged from infested cut wood from Ravenswood, Chicago, IL, or Bayside, Queens, NY, and were held at $25 \pm 2^\circ\text{C}$ and $60 \pm 5\%$ RH. NM = Norway maple, RM = red maple, SM = sugar maple, VM = silver maple, and ash of unknown species.

emerged, in addition to the population they came from, but not the interaction between the two, had a significant effect on their fecundity, the number of pits they chewed in the bark, and their weight, but no significant effect on their longevity (Fig. 8). For the Illinois population, fecundity, longevity, and mean emergence weight were greatest for females that emerged from ash compared with Norway and silver maple. For the New York population fecundity was greatest for females that emerged from red maple. There were no significant differences between the populations in the diameter of the branch sections they emerged from (although the branch sections obtained were highly variable in diameter) or the population density as measured by number of adult emergence holes in the log or number of oviposition pits chewed in the bark. The sugar maple logs were, however, of a significantly larger diameter (11.2 ± 1.9 cm, $\alpha = 0.05$, critical t value 1.988, LSD Statistix 1998) than all the other logs (red maple 9.0 ± 1.8 cm, silver maple 9.5 ± 2.5 cm, and ash [species unknown] 7.5 ± 0.7 cm) except the Norway maple (10.0 ± 2.4 cm). No significant relationships existed between branch section diameter and fecundity or longevity for the adults that were part of these studies.

Discussion

Individuals from the Illinois and New York populations were significantly different in some key reproductive traits. The Illinois females were significantly more fecund than those from New York when they emerged from infested wood and tended to be more fecund when reared on artificial diet. Egg viability was similar when they came from infested wood but the New York population tended to have a higher viability when both were reared on artificial diet. Weights of adults reared from wood depended on the host species involved but when reared on artificial diet the Illinois adults were significantly heavier than the New York adults. This weight difference directly translated into a higher fecundity for the Illinois population because the longevity of adults was not significantly different between the two populations.

The two populations also had slightly different oviposition strategies. The Illinois females laid more eggs during the peak egg-laying week and their oviposition declined faster than those from the New York population in both generations. Although branch section handling (amount of drying time and length of chill received before cutting) varied for beetles from the

first generation it was uniform for the second generation and so does not explain the differences observed. The more concentrated egg laying period of Illinois females may have been an adaptation to deal with a shorter warm season in Illinois than in New York, where females must start laying eggs as soon as possible and complete oviposition sooner, especially when they emerge later in the season. Alternatively, it may be an indication that the two populations were initiated from individuals that came from different parts of China that had different climates. Another difference in oviposition strategy between the two populations was that the New York females used a greater percentage of the pits they chewed to lay eggs in than did the Illinois females. This may have been an indication that the New York females will accept a broader range of host quality conditions than the Illinois females. This could even be manifested in a wider host preference. An alternative possibility was that the New York females are more easily distributed when logs were checked daily for pits and may have stopped laying an egg in a pit they had chewed and did not return to the pit to lay an egg.

Anoplophora glabripennis, in general, laid more eggs and survived longer in the laboratory on *A. saccharum* and other host species (Smith et al. 2001) than has generally been reported (Haack et al. 1997, Milius 1999). Females laid an average of 50–75 eggs and survived an average of 73–88 d on *A. saccharum*, depending on the larval food source and population the beetles came from. The maximum longevity for a female was 123 d and the maximum fecundity was 170 eggs, both for Ravenswood females reared on artificial diet. During the third week after mating, up to five eggs a day were deposited.

Reports of fecundity and longevity for other *Acer* species are varied. He and Huang (1993) reported 32 eggs per female on *A. negundo* at 27°C. Field-collected females have been reported to live for an average of 46 d on *A. negundo* (Gao and Zheng 1998). The lower fecundity and longevity reported in these other studies may have been due to the presence of factors that led to earlier beetle mortality. Adults obtained from infested branch sections from Chicago, IL, laid an average of 193 and 98 eggs and lived an average of 103 and 97 d on *Acer platanoides* L. and *Acer rubrum* Medwedew, respectively, in the laboratory (Smith et al. 2001). The higher fecundity and longevity in the study by Smith et al. (2001) are likely due to holding the oviposition bolts and twigs in moist sand or water when presenting them to the adults, which has been shown to both maintain the moisture level and elevate the nutritional quality of the woody material (Shibata 1998), or to providing leaves as an additional food source that may contain nutritional components not found on the twigs. Higher fecundity and longevity may be possible on *A. saccharum* under similar conditions. This emphasizes the importance of not only host species but also host quality on fecundity and adult longevity.

Larval food source and quality also affected female fecundity and longevity. Both fecundity and longevity

were higher for females from both populations when larvae were reared on a high nutrient artificial diet than when larvae completed development in cut branch sections. In addition, the two females that emerged from *Fraxinus* sp. were significantly more fecund than those that emerged from *Acer* sp. and there were differences between the *Acer* sp. in fecundity for the New York population (Fig. 8). Some of the differences between the populations may have been due to the timing of the tree cutting at the two infestation sites. *Monochamus carolinensis* (Oliver) larvae that developed in bolts cut during the spring were larger and more fecund than those that developed in logs cut during the summer or fall of the same year because of nutritional differences in the wood (Akbulut and Linit 1999). The Illinois branch sections were cut in the winter and the New York branch sections were cut in the spring. This could account for the larger size of the New York adults in the first generation compared with the Illinois adults. Phloem density can affect adult female longevity, fecundity, and size in other Coleoptera species (Haack and Slansky 1987). Differences in cut branch section drying rates between tree species also may have affected adult weights, which in turn affected fecundity, as has been shown for other Coleoptera (Haack and Slansky 1987). The denser maple branch sections (*A. saccharum* and *A. platanoides*) appeared to dry and crack sooner than the less dense branch sections of *A. rubrum* and *A. saccharinum* L. Adult weights tended to decline as the branch sections dried, especially for the hosts with denser wood. This implies that the nutritional quality of the host in which the larva develops may have as great an impact on adult fecundity and longevity as the host species itself.

The number of oviposition pits the female chews also may be related to host quality and species. Females have been observed chewing pits on *A. saccharum* even if the bolt is completely dry when no other host material is present (unpublished data). Females also chewed several pits the first week (after emergence) while they were conducting maturation feeding and laid few if any eggs. During this time, the females may check host quality, inner bark moisture level, and nutritional quality by chewing the pit and then choose to lay an egg only if it is acceptable. The factors involved in determining host acceptance for oviposition likely have a genetic basis resulting in variation between females, as was observed, and are functionally expressed as a polygenic threshold trait that would fit the hierarchy—threshold model proposed by Courtney and Kibota (1990). In addition, many of the small diameter bolts provided for oviposition had thin bark similar to the twigs and the females may have fed on the bark of the small bolts in the same way they did the twig bark. Some of the pits counted were more than slits and may have been feeding sites rather than oviposition pits. *Acer saccharum* has a high sugar content compared with other hosts and sugar content has been positively correlated with feeding, longevity, and fecundity (Gao and Zheng 1998). Li et al. (1999) found that adults would feed on the trunk

of *A. saccharum* in addition to the bark. Finally, females could have been disturbed during the process and never attempted egg laying. These factors combined may account for the high percentage of pits chewed that never had an egg laid in them. The results of Smith et al. (2001)—that >90% of the pits they considered to be for oviposition had eggs laid in them—are further evidence that host nutrition or moisture levels may be important in choice of egg laying sites.

Egg viability on *A. saccharum* was higher than or equivalent to that reported for *Salix*, *Populus*, and other *Acer* species (He and Huang 1993, Zhao et al. 1999) and remained high throughout the female's life. The lower lifetime percent egg viability in the second generation compared with the first generation could have been due to the effects of larval rearing on artificial diet or to lower than normal precipitation during that summer compared with the previous, resulting in the oviposition bolts being drier when cut. When eggs are held under conditions that are too dry they may not hatch even when they are fertile (unpublished data). The lower egg viability reported in the studies of Smith et al. (2001) may be due to either host suitability or moisture level. Although holding bolts in moist sand can increase fecundity (Smith et al. 2001), the eggs laid may not hatch as well due to the higher than normal water content of the inner bark. High moisture content of bark has been proposed as a possible tree resistance mechanism against *A. glabripennis* in some species of poplars in China (Qin et al. 1996). In addition, host callus formation around eggs has been observed to crush eggs in *A. rubrum* (unpublished data).

A little over 1 wk of preoviposition feeding was required before egg laying began. The length of this period was not affected by the timing of mating within that time frame. If females were mated after the preovipositional feeding period had been completed, fertile eggs were laid within 24 h of mating. In one case, two females were inadvertently "mated" and about twice the number of eggs (infertile) a single female would lay were deposited starting in week 2 and egg laying continued for several weeks until the first bolts were stripped and the problem was found. Thus, if females have a bolt on which to oviposit and have contact with another adult they can begin oviposition without mating.

These differences between the two populations and the host quality and host species effects on fecundity and longevity may have management implications. For example, even though ash trees tend not to be heavily attacked in the infested areas when more preferred hosts are present, ash species should be included in survey protocols, because females that do develop in them tend to be more fecund and live longer. Further studies to delineate other life history and behavioral differences between the populations and understand the inheritance of these differences should be carried out to determine if different management strategies need to be employed at the two infested sites. Regardless of these population differ-

ences and the effects of host species on adult longevity and fecundity, the implication of these findings is that under favorable conditions (optimal hosts and low mortality factors) *A. glabripennis* can lay substantial numbers of eggs over a relatively long life. It will be important for control and eradication measures to find ways to kill adults before emergence or very soon thereafter to prevent spread and population increases.

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